

XEROPHYTISM IN THE SWAN RIVER DISTRICT.

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The term xerophyte is applied to plants capable of thriving in an environment unable to provide a normal plant with a sufficiency of suitable water. Such plants may be found in quite widely differing regions. Hot deserts, arctic, antarctic and alpine lands, acid swamps, beach or salt-lake areas, all offer plants very limited supply of suitable water during the whole or a large part of the year. The ice-bound portions of the earth have no liquid water available for plants, while beaches, salt-lakes and swamps usually provide only water charged with injurious substances.

The Western Australian bush is crowded with xerophytes. Our rainy season plants must not be included, however, for they either pass through the whole of their lives in the months of rain or else lie dormant underground as bulbs, corms, rhizomes or tubers during the season in which their aerial portions are unable to withstand the hot drying influence of our summer sun.

The xerophytic vegetation is of another type. It provides the permanent flora and comprises those plants which are able to withstand the whole round of the seasons for perhaps many years. In our ten, nine, and even eight inch rainfall belts, dense assemblages of plants are found, here and there rising to the dignity of forests, and the plants so met are all able to flourish throughout the months of the year in which the precarious replenishment of water supply is dependent on occasional thunder showers. Even the poorly retentive sandy soils carry their cloaks of vegetation.

The secret of this continued existence in such a forbidding environment is revealed by a study of the morphology and anatomy of the plants. Numerous departures from normal structure are to be noted and these are concerned with (a) absorption, (b) storage, and (c) loss of water.

With regard to absorption, the root system is usually highly developed. Sometimes it is the great depths of the soil which are searched for water, while often an up-rooted gum tree shows an extended surface network of roots, eminently fitted to absorb rapidly the moisture from short summer storms. In addition, curiously modified hairs, capable of absorbing dew deposited on the plant surfaces, are occasionally to be seen.

Water storage tissues are to be found in all parts of plants. Bulbous roots such as those of *Droseras*, swollen stems of some salt-bushes¹ and fleshy leaves of the "pig-face,"² all furnish

1. *Salicornia Australis*. 2. *Mesembryanthemum Aquilaterale*.

examples. In many of our xerophytes, too, the epidermal cells are of considerable size and contain an appreciable reserve of water. This is particularly noticeable in the "ice plant."³

Chief plant activity, however, has been directed towards minimising transpiration. Loss of water is a source of grave danger to most of our bush plants. If the rate of such loss exceeds that at which absorption proceeds, the plant is forced to draw on its water reserves. Should these become depleted, growing tips of roots and shoots lose power of growth, drooping commences and still further desiccation results in permanent injury or death. But transpiration is a necessary danger. In plant nutrition, constructive metabolism demands at least seven soil constituents. These can be obtained only in solution by the absorptive system of the plant. The continuous supply of these soil constituents is dependent, then, on the steady inflow of soil water. Since the water-holding capacity of any plant is limited, it follows that the uninterrupted entry of dissolved minerals is dependent on provision being made for the escape of water from the plant surface. Water loss, therefore, is necessary. In humid climates, where evaporation is exceedingly slow, certain plants (*Tropaeolum majus* and *Fuchsia*) exhibit structural modifications which allow the exudation of water from definitely placed pores. In our dry season, however, hot dry air, renewed by almost constant winds, accelerates the rate of evaporation to such an extent that even the hardiest of our introduced garden plants needs the constant care and protection of the gardener.

Normally, transpiration is not permitted to take place over the whole area of the plant. A waterproof cuticle restricts it to the stomata on the green portions, and in the corky regions lenticels are provided. To the lenticels of our plants I have paid but little attention. They certainly are not prominent features and probably are poorly developed. Moreover, it is to the neighbourhood of green surfaces that the transpiration current brings the materials required in the metabolism following on photosynthetic activity. Stomata are most numerous on leaf surfaces and therefore it is to the leaves of xerophytes that we look for the chief evidences of modification.

I have selected at random the leaves of a few of our plants, and a study of stained sections shows how their anatomy specially enables them to guard against excessive loss of water vapour.

1. *Banksia attenuata*.

Plate XV., Fig. 1, shows the typically bifacial structure exhibited by a transverse section of a leaf of this plant. Stomata

are restricted to the shaded underside, and there, free circulation of air is prevented by a dense layer of short, curly hairs. These are present in such numbers as to give the lower surface of the leaf a white colour. Another xerophytic structure is the layer of mechanical fibres underlying the upper epidermis. These fibres remove the softer mesophyll tissues from the dry atmosphere and give a noticeably hard texture to the whole leaf.

The reduction of the softer tissues from which evaporation is liable to take place is characteristic of xerophytic plants. Their replacement by sclerenchyma renders the vegetation harsh and gives a profusion of spines, prickles and thorns.

Dryandra Floribunda.

Plate XV., Fig. 2, shows a transverse section of a leaf of this plant. On the under surface of each leaf there are numerous pores leading into spacious flask-like cavities hollowed out in the spongy parenchyma. Stomata are restricted to the inner surfaces of these cavities. The remaining external surfaces are protected by a thick waterproof cuticle. As a result, the stomata are not exposed directly to the sun's rays and the air on to which they open is changed exceedingly slowly and soon becomes almost saturated with water vapour. Evaporation through the stomata, therefore, is greatly retarded. The efficiency of the system is still further enhanced by numerous hairs which arise from the epidermal cells lining each cavity and which produce a plugging effect at the pore-like opening.

The mechanical tissues of the leaf are strongly developed, a layer of sclerenchymatous fibres underlying the epidermis, increasing the distance between the softer tissues of the mesophyll and the leaf surface. This lessens the tendency for evaporation to occur, tempers the brightness of the sunlight and at the same time makes the leaves so hard that they feel like thin chips of wood.

A slightly contradictory feature is the lens-like appearance of the epidermal cells overlying the groups of palisade cells. It would seem that they function in concentrating the light on the assimilation tissue beneath, but probably they serve chiefly as water reservoirs close to the regions of greatest photosynthetic activity.

Ammophila Arundinaceae.

The next xerophyte to be mentioned is *Ammophila arundinacea*, Host (the Marram Grass), examples of which may be found growing close to the beach near Perth. Although not an indigenous plant, it is so well established as a naturalised alien that it is not out of place to mention it here. This grass I first gathered with other plants at the Oshorne Rifle Range. On examining the long

linear leaves later, I was surprised to find them tightly rolled into the form of a straw, tapering to a point. Transverse sections of the leaves appeared as shown in Fig. A of Plate XVI.

On the upper surface of the leaf are pronounced flattened ridges separated by furrows. A smaller more wedge-shaped ridge divides each main furrow into two secondary furrows. The section shows that the ridges are due to girders of sclerenchyma, one being formed along each vascular bundle. The vascular bundle exactly resembles that of maize. The mesophyll consists of a compact parenchyma, slightly differentiated into columnar cells on the lower (outer) surface. Intercellular spaces are practically wanting. A small air cavity exists behind each stoma, but no other spaces are seen in a transverse section. There is therefore little cell surface exposed to an internal atmosphere and, consequently, evaporation is limited. On the other hand, no cell is more than three or at most four cells removed from the air cavity of a stoma and so can obtain by diffusion any carbon dioxide required for photosynthesis. The epidermis of the outer surface has a strongly developed cuticle and the lens-like enlargement of epidermal cells for light concentration and water storage is well shown.

Chief interest, however, is centred about the abnormal epidermis of the inner surface of the leaf. On the summits of the girder-like ridges the epidermal cells are small, frequently conical, or else produced into stout conical hairs. In the secondary furrows the epidermal cells are enlarged into thin-walled sacs, often conical, containing large water reserves and with bases in close contact with the compact mesophyll. Cuticle is but slightly developed in the furrows.

On excessive transpiration causing an undue loss of water, the enlarged epidermal cells (which we can call the "Curvature Tissue") in the furrows become less turgid, and shrinking, diminish the length of the epidermis stretching across the furrows. The width of the whole epidermis of the upper side of the leaf is diminished. At the same time the compact photosynthetic mesophyll contracts, water loss causing shrinkage of cells not separated by air spaces. Since the outer epidermis, protected and strengthened by its tough cuticle does not similarly alter in dimension, a curving takes place, each furrow and the whole of the inner surface of the leaf becoming more concave. Should the water deficiency continue to increase the furrows are obliterated gradually by the approach of the side walls and the whole leaf is tightly rolled. In plucked leaves this change takes place with great rapidity, curvature being marked in five minutes. This indicates that in the expanded position of the leaf transpiration is rapid, the plant by leaf movement being adapted to either dry or wet conditions. It is a plant well fitted for life in our climate of

seasonal extremes. Fig. A of Plate XVI. shows a leaf partially curved, while Fig. B is a more highly magnified view of the curvature tissue lining a secondary furrow.

The closing of the furrows (into which the stomata open) prevents circulation of air in the pit-like entrances to the stomata, and this end is further served by the interlocking of the stout hairs which grow in greatest profusion at the edges of the longitudinal ridges. Finally, on rolling being completed, the furrows themselves open on the closed cavity contained by the rolled leaf. There is then a most striking and successful attempt to protect the plant from excessive transpiration.

On the checked transpiration allowing the plant to make good by absorption the undue water loss, the cells of the curvature tissue and the green mesophyll regain their turgor and the leaf unrolls.

Reference to the structure exhibited by an oat leaf is informative with regard to the origin of the specialised structures of the marram grass leaf.

Leaf of Xanthorrhoea preissii.

The long brittle, prismatic leaf of this plant is anatomically divided into two distinct zones.

The outer layer, shown as a narrow border in a transverse section (Plate XVII.) contains the chlorophyll-bearing cells and much sclerenchyma. This latter tissue forms girders, triangular in section, running in the direction of the length of the leaf, the broad bases forming a rigid support for the epidermis. The outermost layer of sclerenchyma, one cell thick, is marked off from the remaining portion of this tissue by taking acid fuchsin stain more feebly, and consequently stands out as a light line between the epidermal layer and the cells situated more deeply. It also runs continuously, forming a connecting link between neighbouring girders of sclerenchyma. The chlorophyll-bearing cells form columns of palisade tissue lying between the sclerenchyma strands, and are crowded with polygonal chloroplastids. In the transverse section, the palisade tissue appears as a series of scallops around the margin of the leaf, each portion of it being so placed with respect to the sclerenchyma that the light is much tempered. The epidermis is composed of conical cells, the cavities being much encroached upon by thickenings of the cell walls. A cuticle is strongly developed. The stomata are well protected by clusters of blunt hair-like outgrowths of the epidermis. Another distinctive feature is the lining of the stomatal cavity by a continuation of the outer layer of sclerenchyma mentioned above. In this region, however, many of the fibres are irregularly formed and fissures

appear between them. An interchange of gases between the external air and the palisade cells is therefore permitted, but to a restricted extent. In addition, the palisade cells fit compactly together, so the loss of water vapour must of necessity be slow.

The inner region of the leaf contains large parenchymatous water-storing cells, but loss of water to the outer border is restricted by the interposition of a row of mechanical fibres. The portion of the section within these fibres has a structure somewhat similar to that of a monocotyledonous stem. Vascular bundles appear throughout the section. On examination it is seen that they are not scattered indiscriminately, but appear in more or less definite lines seen running laterally across Fig. A of Plate XVII. As in *Zea mais*, each bundle is enclosed in a sheath of mechanical tissue. Within this are two distinct sets of xylem cells forming a "V" and almost meeting at the apex which is directed towards the central parts of the leaf. The outer ends of the xylem sets enclose the phloem, which is cleft in two by a median strand of sclerenchyma. The bundles nearest the leaf surface are imperfectly formed, being in fact the ends of vascular strands which occupy a more central position in a section at a lower level of the leaf. Two such bundles are shown in Fig. B, Plate XVII., and in them the xylem sets are not well marked. Each bundle is so oriented that the phloem is directed towards the nearest surface of the leaf.

The chief xerophytic characters shown in the leaf structure of the Blackboy are:—

- (1) Water-storage tissues in central portions of leaf.
- (2) Prevention of excessive transpiration by—
 - (a) limiting of stomata to strips of leaf surface overlying the palisade cells;
 - (b) a thick cuticle;
 - (c) removal of delicate parenchymatous cells from epidermal layer by the interposition of much sclerenchymatous tissue;
 - (d) Minimising water loss through stomata by blunt hairs, narrow entrances, and an almost continuous layer of woody fibres which separates the stomatal cavity from the parenchymatous cells below.
- (3) The water distributing xylem elements of the vascular bundles are strongly developed.

Each leaf examined shows some adaptation for water conservation, and though in many leaves the structural features are very similar, it happens that now and again some rarer device is displayed. The origin of these features to which the plants owe

their continued existence affords ground for most interesting speculation and is intimately connected with the history of our portion of the Australian continent.

The land surface of south-west Australia is an old one, having maintained its position during earth changes which have caused other land masses to be raised above or submerged below the ocean waters. In addition, through a very great period of time, there has been a continued isolation from other land regions. As a result, our flora (and fauna also) has in large measure been able to maintain a certain air of primitiveness. Associations of she-oaks,⁴ blackboys,⁵ banksias,⁶ seem to afford us glimpses of the vegetation which has long since passed away from other portions of the earth. (On the other hand it has to be borne in mind that others of our plants—lilies, orchids, compositeae, etc., show the same structural development met with in other continents, but these are annuals or have no aerial portions during the dry season. In fact, although not xerophytes, their life histories are perfectly adapted to their climatic environment.) But, undisturbed by alien plant invasion, the local flora has been subject to disturbing attacks of quite another nature. The great antiquity of our land has enabled it to experience profound climatic changes. Even north in the tropics we find the records of past glacial activity, but the change which has done most to determine the present type of our flora has been a prolonged period of slow desiccation. Physiographical evidence indicates that the major portion of our wheat belts, now dependent for summer water on artificial storage of the winter rains, once formed portion of the well watered valleys of a huge drainage system, the main river of which was a mighty stream, estimated by some to have risen in the Murchison region and to have entered the sea at a coast line approximating to our present-day south coast. It is probable that the old river levels assisted largely in the grading of the Great Southern Railway. Apart from this, weakly streams such as the Chapman River have a flow of water quite incommensurate with their large rock-cut valleys, while other ancient river valleys are shown only by exposure of fluvial deposits such as those in the railway cutting near Mullalynp. Physiographic evidence also shows that at least on two and perhaps on three occasions, after large land uplifts, drainage systems were able to reduce the land surface to a peneplain at sea level.

The deduction following these facts is that at some remote time, the flora of a large part of Western Australia must have been in equilibrium with climatic conditions largely determined by a plentiful water supply. Such mesophytic and hygrophylous

4. *Casuarina Fraseriana*.

5. *Xanthorrhoea Preissii* or *X. Reflexa*.

6. Commonly

Banksia Menziesii.

plants must have included the ancestors of the present day species, and probably also other types, the descendants of which have become extinct. Fossils from portions of our inland South-West and Great Southern areas have proved to be remains of Laurineae—cinnamon-like plants—which almost certainly lived in a moist tropical or sub-tropical climate. Horizons of coal measures, partly lost by denudation, are being exposed over increasing areas, and these, too, furnish some evidence of ancient floras and environments.

On the living materials (probably the chromosomes in particular) of the ancestors of our xerophytic plants, drying climatic conditions exerted a new set of stimuli. The development of certain characteristics met with repression whilst others, so checked by the old order of conditions that they were not able to be evidenced at all, slowly made their appearance owing to either the stimulation or lack of repression of the new external environmental factors.

In some instances, doubtless, the changes induced in the plants were not beneficial. The resultant state of a plant so modified would leave it to adjust itself to changing conditions with no means for so doing. In other cases, the changes may have been inimical, with the result that necessary functions could be carried on but imperfectly. Whichever the case, changes being inimical or merely immaterial, the effect would be evidenced in a retarded rate of reproduction, natural selection ultimately leading to extinction of the plant in regions of appreciable environmental change.

It is certain that in the cases of at least some of the ancestors of our xerophytic plants, beneficial alteration of characteristics followed modification of environment. Buffon, advancing the idea of variation of species, and Erasmus Darwin, of the inheritance of acquired characters, first led modern thought towards the great truth of progressive evolution. In the light of this truth, we may believe that here in this State, through very many hundreds of generations, progressive change of structure followed the gradually changing water relationship. Such progressive modification, established in the cases of many organisms, is capable of effecting quite drastic structural alteration within that portion of geological time to which fossils give us reference, and such change is almost certainly responsible for much of the specialised anatomy and morphology of our xerophytes.

Some of the plants actually indicate in the individual the progressive development of their race. The first leaves of seedlings, differing from those of the mature plant, probably resemble the ordinary foliage leaves of remote ancestors. In the case of wattle seedlings, it may be noticed that the first leaves are bipinnate, like

those of a typical acacia. Those formed next show some reduction in the surface area of the small leaflets, while a compensating expansion of the leaf stalk enables photosynthetic activity to be maintained. Lastly, foliar growths consist of expanded leaf-stalks only, no trace of the acacia-like leaflets being displayed. We here see each individual climbing its genealogical tree, showing clearly a progressive reduction of leaf surface, which must have accompanied the growing aridity of environment.

It seems, then, that external factors are able to affect the body tissues. These, in their turn, must influence the metabolism of germ-plasm and so cause variation from generation to generation.

A Darwinian progressive variation such as that suggested above does not exhaust possible explanation of the origin of xerophytic structures. Change of external conditions, or wide interspecific crossings, may cause changes in number, function or chemical composition of chromosomes or more general changes in the protoplasm of a cell or cell nucleus. The progeny of plants so disturbed exhibits abrupt and distinct character changes, not wholly explainable by any regrouping of old characters. The evening primrose, *Oenothera lamarckiana*, carried from the New World to the Old, was thrown by the change into some state of nuclear instability. Three varieties appeared, each breeding true. Variety *gigas* has twenty-eight chromosomes instead of the normal fourteen, and has an accompanying structural characteristic, a greatly increased size. Variety *semigigas* exhibits the triploid number of chromosomes, whilst variety *lata* has fifteen. Environmental change has been accompanied by nuclear disturbance, an outward sign of which is the changed structure of the individual.

Luther Burbank, experimenting in specific plant crosses, produced entirely new varieties of plants. The union of species of dewberries and raspberries resulted in the primus and phenomenal berries—fruits with new size, colour, texture, and taste characters. These proved to breed true. The plumcot, a cross between plums and an apricot, does not appear to have become fixed.

In nature, combinations of circumstances are known to produce mutants. Darwin, calling them "sports," attached too little importance to them in his view of biological evolution, while De Vries, passing to the other extreme, held that evolution had progressed solely through their instrumentality. Both views have proved narrow. Xerophytes have developed in each way, and, should a complete suite of Western Australian fossils ever be available, some plants will be traceable, step by step, back to their hygrophilous ancestors, whilst others will prove to have assumed drought-resistant characters in an abrupt manner.

One further phase of xerophytism remains to be mentioned, and that is its relationship with plant parasitism. A profusion of cassy-

thas, the Westralian Christmas Tree,⁸ the Sandalwood Tree,⁹ the Quandong,¹⁰ and Australian Mistletoes,¹¹ all make our bush a veritable botanic garden of parasitic plants.

This plentitude of parasites in our xerophytic plant assemblages is worthy of note. It may be that the parasitic habit is as much (or perhaps more) due to the aridity of environment as to the stimulus of nitrogen search. The emphasis is still further removed from the nitrogen-seeking stimulus when it is remembered that in Westralian soils the essential soil constituent present in minimum amount is phosphorus—not nitrogen. Of course it may be shown that many of the parasites remove nitrogen containing compounds from their hosts, but this, though now of great importance to the parasite, may be quite a secondary phase of the habit.

Again, in some instances, it may be noticed that a cassytha puts out haustoria at places which are not in contact with any host. The parasitic attack must in these cases be an act innate in the parasite and not dependent on external stimulus. With evidence of such a change having been accomplished, it does not seem right to ascribe the origin of parasitic habits to nitrogen-seeking simply because a parasite may be shown to derive nitrogen from its host.

Thus, although usually regarded only in its nitrogen relationship, plant parasitism in Western Australia possibly originated as a modification capable of adjusting some disparity between water absorption and water loss. The securing of nitrogen would be at first a non-essential concomitant of successful attempts to secure water from better provided neighbours, and the highly specialised parasites exhibit the ultimate developments of a trend of evolution which originated in some stimulus of water relationship.

References to plates.

- C. = stomatal cavity.
- C.T. = curvature tissue.
- Cu. = cuticle.
- E. = epidermis.
- G.C. = guard cells.
- H. = hairs.
- L. = lens-like epidermal cells.
- M. = mesophyll cells.
- M.P. = palisade mesophyll.
- M.S. = spongy mesophyll.
- Sc. = sclerenchyma.
- S.F. = secondary furrows.
- S.P. = stomatal pit.
- V.B. = vascular bundle.
- W.P. = water-storing parenchyma.
- X. = entrance to furrow.
- Y. = air above leaf becoming enclosed by rolling.
- F. = fibres underlying epidermis. (In Plate XVII. layer is almost continuous below stomata.)
- Fi = fibres surrounding water-storage tissue.

8. *Nuytsia Floribunda*.

9. *Fusanus Spiratus*.

10. *Fusanus Acuminatus*,

11. *Toranthaceae*.

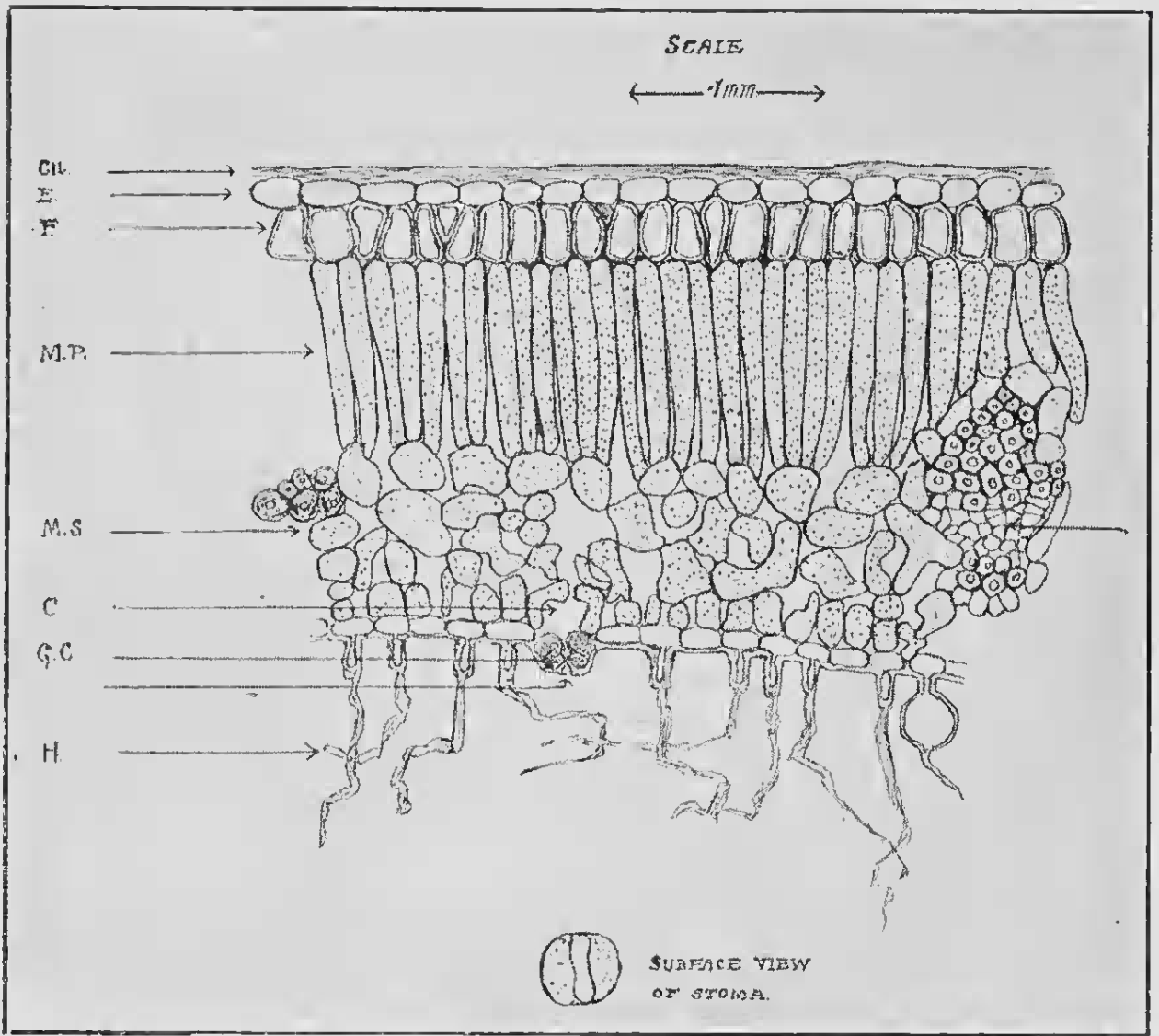


Plate XV., No. 1.—Leaf of *Banksia Attenuata*.

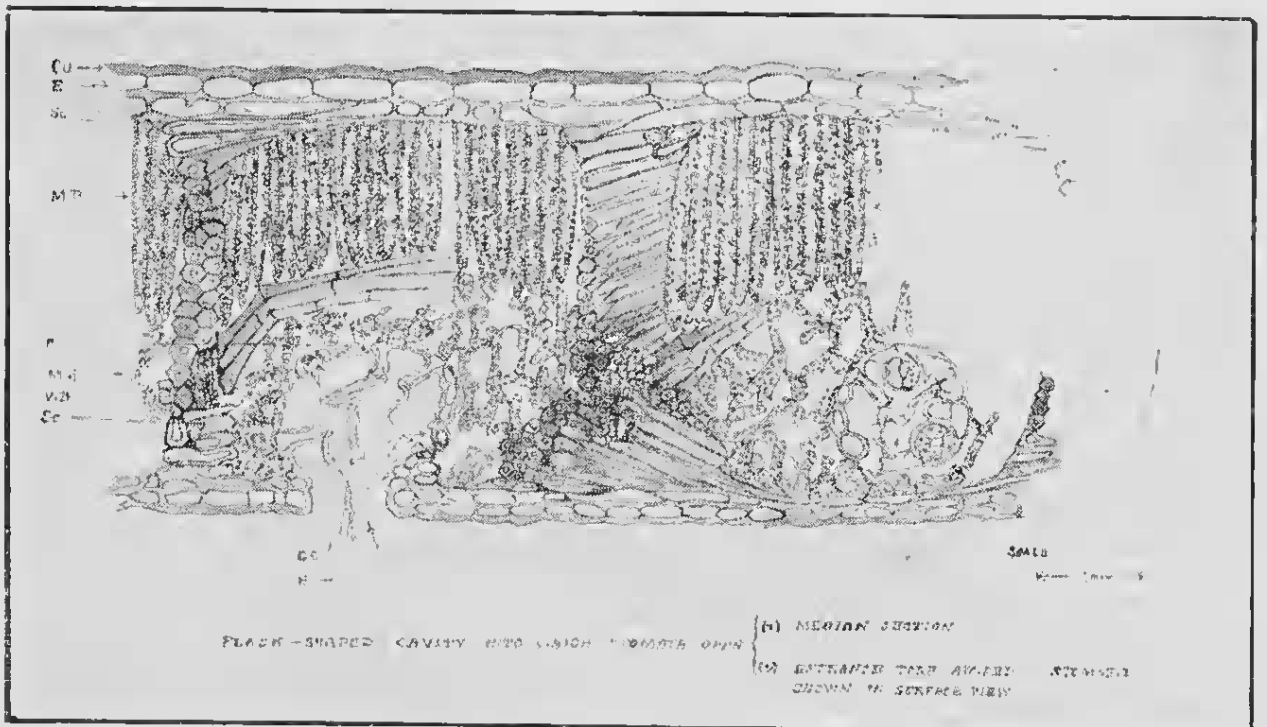


Plate XV., No. 2.—Leaf of *Dryandra Floribunda*.

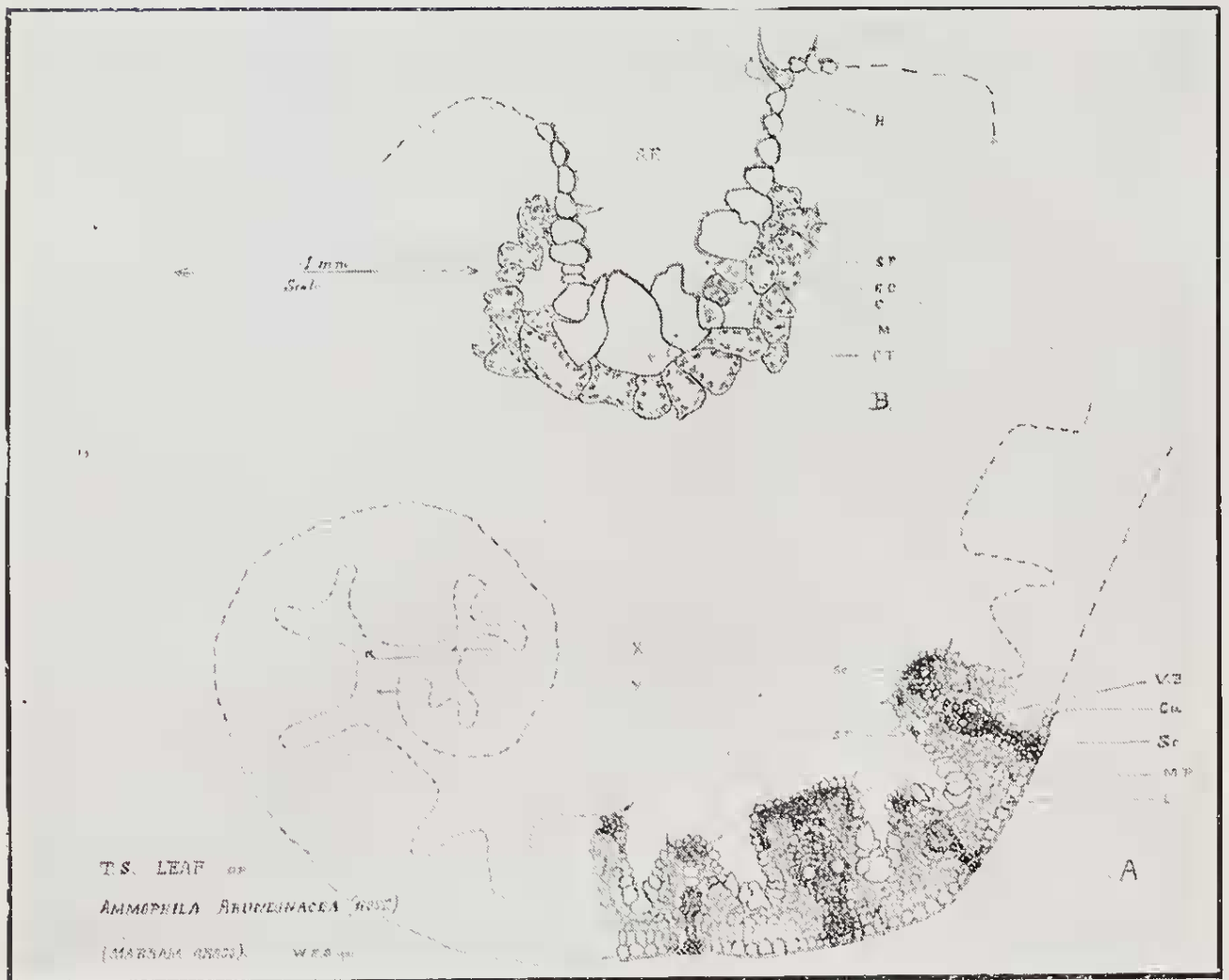


Plate XVI.—Leaf of *Ammophila Arundinacea*.

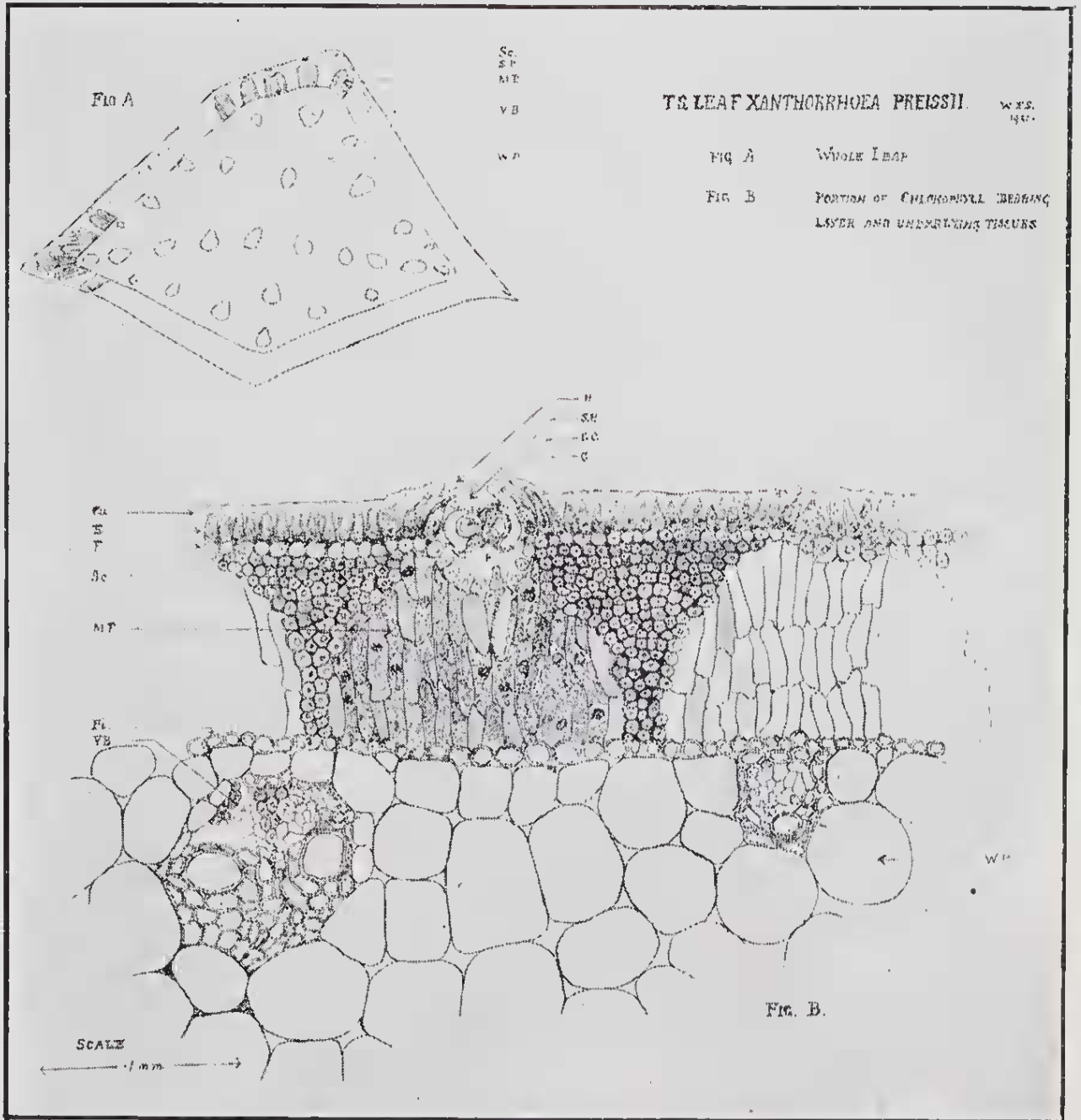


Plate XVII.—Leaf of *Xanthorrhoea Preissii*.